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Sugarcane leaf area development under field conditions in Florida, USA[☆]

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Abstract

Leaf area development is critical in the establishment of a full leaf canopy to maximize interception of solar radiation and achieve high crop productivity. In sugarcane, leaf area development is especially important because the rate of leaf area increase is relatively slow. Previous studies have highlighted the fact that the rate of emergence of individual leaves is highly dependent on temperature. These previous studies have been limited, however, to only very few cultivars, and these cultivars were adapted for production in environments different from the climate of the continental USA. Hence, there is little information for cultivars selected for production in other environments and little basis for resolving which variable contributing to leaf area development has the greatest impact on canopy leaf area. The objective of this 2-year field study was to examine the contribution of rate of leaf emergence, leaf shape, and individual leaf area to the development of plant leaf area. Four cultivars developed for the subtropical climate of Florida were compared. The dependence of leaf emergence as a function of temperature was confirmed in this study and the leaf appearance rate of CP88-1762 was significantly greater than CP72-2086. Leaf shape was found to be nearly uniform among the four cultivars although the shape factor (0.72) was different from that previously reported for sugarcane. Cultivars differed in the area of successive emerged leaves on the stalk. Leaves produced early in development were found to be larger for one cultivar (CP88-1762) as compared to the other cultivars. These results indicated that area of earliest leaves produced by sugarcane cultivars might be a variant that could be exploited to achieve more rapid development of crop leaf area.

Keywords: Sugarcane; Leaf area; Leaf emergence; Temperature response

1. Introduction

Leaf area development is crucial in crop production to maximize interception of solar radiation and accumulation of crop mass. Slow development of leaf canopies may be critical in limiting the ultimate yield produced by sugarcane crops (Inman-Bamber, 1994). This may be particularly true for sugarcane grown in the continental USA where the crop is harvested

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annually and the initial growth of both plant crops and ratoon crops occur during winter and early spring months when low temperatures may result in substantial restriction on the rate of leaf area development.

The rate of leaf appearance is strongly dependent on air temperature (Inman-Bamber, 1994; Campbell et al., 1998; Robertson et al., 1998; Bonnett, 1998). In previous studies, the first leaves produced on the plant appeared at a relatively high rate as a function of cumulative temperature after subtracting a base temperature from daily mean temperature, but later leaves appeared at slower rates. This leaf appearance pattern has been characterized as a biphasic response with linear rates of appearance on either side of a break point. The break point has been reported at leaf #14 in a study of two cultivars (Inman-Bamber, 1994) and at leaf #10 in a comparison of nine cultivars (Bonnett, 1998).

The applicability of the previous studies to describing leaf area development for the cultivars grown in the continental USA is of concern because prior investigations were done using almost exclusively cultivars developed for different climates and long-growth cycles. The one exception was a cultivar developed in Florida (CP51-21) that was included in the comparison done by Bonnett (1998). In that study, CP51-21 had one of the fastest rates of leaf production. Whether CP51-21 is representative of other cultivars developed for subtropical growth, and whether the assumed base temperature of 8 °C is appropriate for subtropical cultivars were untested.

To fully resolve the leaf area development, and ultimately crop growth, of sugarcane grown in subtropical USA, several critical traits needed to be re-examined. The objectives of this research were to examine these traits including the base temperature for leaf appearance, rate of leaf appearance, leaf shape factor in calculating leaf area, and plant leaf area development. The observations were made during two growing seasons on plant and ratoon crops grown under field conditions. The study was done on four cultivars and at three locations in Florida.

2. Materials and methods

2.1. Plant material

Four cultivars were studied: CP72-2086 (Miller et al., 1984), CP80-1743 (Deren et al., 1991), CP88-1762 (Tai et al., 1997) and CP89-2143 (Glaz et al., 2000). The cultivars were selected for their wide range of phenotypic growth characteristics. CP72-2086 generally takes the longest time to attain canopy closure, CP80-1743 the shortest, and CP88-1762 and CP89-2143 have intermediate early season development rates. The four cultivars were also selected for their importance to FL growers. CP80-1743 and CP72-2086 were ranked first and second in the latest census of FL cultivar acreage (Glaz, 2002), while CP88-1762 (ranked fourth) and CP89-2143 (ranked seventh) have the fastest rate of increase in planted acreage among recently-released cultivars.

2.2. Field layout

A common set of observations on the development of the sugarcane plants was made at three locations. Two locations were in south Florida where sugarcane is commonly grown. One location was at the Everglades Research and Education Center (EC) (26°39′N, 80°38′W), which is 8 km east of Lake Okeechobee and represents a moderate-temperature site during extreme cold temperature episodes. The second location in south Florida was on an Okeelanta farm (OK) (26°26′N, 80°31′W), approximately 36 km south of Lake Okeechobee and this site is comparatively colder during extreme cold temperature events. The soil at these two locations was a Lauderhill muck (euic, hyperthermic Lithic Haplosaprist).

The third location was south of Gainesville, FL (GN) at the University of Florida Plant Science Research and Education Unit (29°24′N, 82°10′W). This location is approximately 500 km north of the area of commercial sugarcane production, but its northern location and cooler temperatures extended the range of temperatures under which plant development was observed. The soil at this site was Tavares sand (hyperthermic, Typic Quartzipsamment, Entisol).

The field layout at all three locations was similar. A randomized complete block design was used with six replicates. Vegetative seed-cane pieces of each cultivar were planted in rows on 24 November 2000 at EC, on 1 December 2000 at OK, and on 7 December 2000 at GN. A replicate of each cultivar consisted of five rows that were approximately 10 m long. The rows in south Florida were spaced 1.5 m apart and at GN they were 2.7 m apart due to machinery limitations.

2.3. Observations

Shortly after emergence of the plant crop in 2001, 10 uniform plants were identified and tagged in each of two interior rows of each plot on one day. At the time of selection only one or two true leaves had fully emerged. One set of 10 plants was used immediately for measurement of leaf appearance from February through May and then harvested. Since the first set of plants was harvested in May, the second set of 10 plants was used for measurement of later leaf emergence in the period from May through August. Due to the slower development of the plants at the GN location, observations were extended 1 month to achieve a similar number of developed leaves at the end of each observation period. Each of the 240 tagged plants (10 plants $\times$ 6 replications $\times$ 4 cultivars) at each location were observed weekly to record the appearance of new, fully developed leaves. Once a leaf had emerged as defined by the appearance of a developed ligule, the date of observation was recorded as well as the width at the widest part of the leaf and the length from ligule to tip. Approximately, leaves #1 through 14 were eventually observed on the first set of plants and approximately leaves #15 through 25 were observed on the second set of plants.

The plant crop was cut and removed from the plots on 22 January 2002 at the south Florida locations and on 26 December 2001 at GN before the plants at this location were subjected to a freeze. The ratoon crop was then allowed to grow from the stubble. The data collection for the ratoon crop in 2002 was the same as was done with the plant crop in 2001. That is, two sets of 10 shoots were identified after emergence in each subplot and these sets of plants were measured sequentially to obtain data on leaf development during the spring and during the summer. Observations were taken weekly at each site on leaves with developed ligules. Leaf length and width were not recorded in this season to expedite measurement.

2.4. Data analysis

The base temperature required to express leaf appearance rate as a function of cumulative temperature was first examined using the spring observations of the plant crop. This analysis was done by calculating mean daily temperature based on the average of minimum and maximum temperatures. These temperatures were extracted from records of temperature recorded at 15 min (EC and GN) or 60 min (OK) intervals by radiation-shielded thermometers positioned at a height of 2 m at each site.

The data collected at GN was used primarily to evaluate base temperature because of cooler temperatures at this location. Lower temperatures at GN resulted in smaller differences between temperature and assumed base temperatures so that the regressions at GN were more sensitive to assumed base temperatures than at the other two locations. The appearance of leaves was regressed against cumulative daily temperature assuming various base temperatures from 9 to 16 °C at increments of 0.5 °C. Similar to the analysis of Inman-Bamber (1994), the assumed base temperature that resulted in a linear regression with the lowest mean square error (MSE) and highest r^2 was taken as the base temperature. The regressions were done for each replicate of a cultivar and mean MSE and r^2 were averaged for each cultivar.

Leaf appearance was regressed for each replicate in each season and year against cumulative daily temperature minus base temperature (cumulative thermal units, TU). The slope of this regression gave the rate of leaf appearance (leaf TU^{-1}); the inverse of the slope is the phyllochron interval (TU). The slope values obtained in each replicate of a cultivar were averaged to obtain the mean value for the cultivars.

Leaf area for each leaf was calculated for the 2001 data from measurements of leaf length and width. First, however, a shape factor had to be determined for each cultivar. One plant from each plot was harvested at the EC and OK sites on 16 April 2002. All non-damaged leaves were removed and their lengths and widths measured. The area of each leaf was measured using an area meter (LI-3000, Li-Cor, Lincoln, NE). The shape factor for each cultivar was calculated as the slope of the linear regression (intercept forced through zero) of leaf length $\times$ width versus leaf area.

The shape factor for each cultivar was used to calculate the area of each leaf of plants monitored through the 2001 season based on measurements of leaf length and width. Consequently, the area for each leaf on each plant could be tabulated. A non-linear regression was used to express leaf area as a function of leaf number on the plant.

Finally, rate of appearance of leaf area was derived from the previous analysis. That is, the appearance of leaf area was estimated by combining the expression of leaf area as a function of leaf number with the expression of leaf number as a function of TU. Consequently, an analytical expression was derived for each cultivar so that comparisons could be made among cultivars in their relative rate of leaf area development as a function of TU.

3. Results and discussion

3.1. Base temperature

The analysis for base temperature was focused on the spring period at GN where temperatures were the lowest. The regression analysis used the appearance data of the first 12 leaves, which was less than the breakpoint previously reported (Inman-Bamber, 1994) so that a linear response was expected. Indeed, a highly linear relationship was found between leaf appearance data and cumulative TU. Linear regressions for all cultivars with base temperature assumed from 9 to 16 °C resulted in r^2 of at least 0.86, as illustrated in Fig. 1 for CP80-1743 at GN. An assumed base temperature of 10 °C in this case, resulted in a high r^2 and fairly small MSE (0.932 and 0.639, respectively).

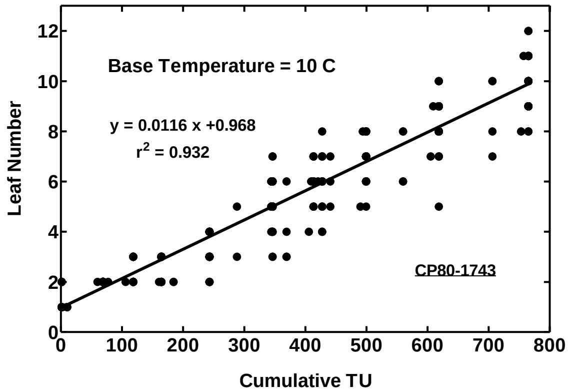

Fig. 1. Increase in leaf number of plants as a function of cumulative thermal units assuming a base temperature of 10 °C. These data are for cultivar CP80-1743 grown at Gainesville in spring 2001 and the regression is based on individual data from all 60 plants.

Selection of the appropriate base temperature was determined as the value which gave the lowest MSE in the linear regressions for each cultivar. A broad range of assumed base temperatures resulted in MSE values that were nearly equal (Fig. 2). The minimum MSE at GN was found at 11 °C for CP80-1743, 10.5 °C for CP88-1762, and 10 °C for CP72-2086 and CP89-2143. These results are consistent with those of Inman-Bamber (1994) who concluded that the base temperature for the two cultivars he studied was 10 °C.

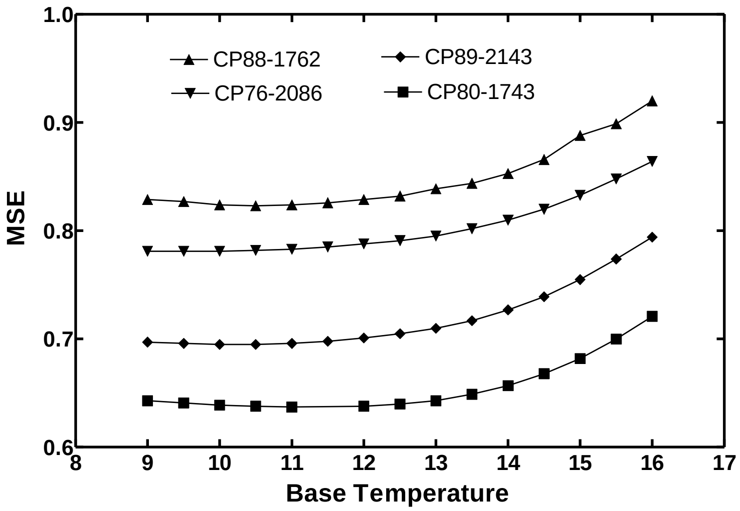

Fig. 2. Mean square error of regressions for increase in leaf number as a function of cumulative thermal units assuming various base temperatures. The results are for each of the four cultivars grown at Gainesville in spring 2001.

Table 1
Leaf appearance rates (leaf TU^{-1}) calculated with a base temperature equal to 10 °C for each cultivar, location, and season

Year	Season	Location	CP80-1743	CP88-1762	CP72-2086	CP89-2143
2001	Spring	GN	0.0113	0.0112	0.0096	0.0113
		EC	0.0101	0.0104	0.0094	0.0098
		OK[a]	0.0133	0.0148	0.0122	0.0123
2001	Summer	GN[a] (drought)	0.0070	0.0086	0.0062	0.0064
		EC	0.0098	0.0099	0.0089	0.0101
		OK	0.0093	0.0093	0.0092	0.0097
2002	Spring	GN	0.0095	0.0107	0.0081	0.0083
		EC	0.0105	0.0118	0.0104	0.0099
		OK	0.0104	0.0106	0.0099	0.0092
2002	Summer	GN	0.0092	0.0094	0.0088	0.0093
		EC	0.0091	0.0093	0.0091	0.0094
		OK[a] (flood)	0.0076	0.0077	0.0074	0.0077
Mean			0.0099 b	0.0103 a	0.0093 c	0.0097 b

Means followed by different letters are significantly different at $P < 0.05$.
[a] Value deleted in calculation of cultivar means.

Since the regression fit for assumed base temperatures was at or near 10 °C for the four cultivars we studied, a common base temperature of 10 °C was assumed for all cultivars in further analyses.

3.2. Leaf appearance rate

The rate of leaf appearance was calculated for each replication of each cultivar. Consistent with the example shown in Fig. 1, a linear fit was found to represent the data in all cases. Further, there was a general consistency across all data (Table 1) with many of the rates of leaf appearance being in the range of 0.0085 to 0.0115 leaf TU^{-1}, or a phyllochron interval of 118–87 TU. These results are consistent with leaf appearance rates reported by Inman-Bamber (1994) for cultivars NCo376 and N12 of 0.0092 and 0.0085 leaf TU^{-1}, respectively (109 and 118 TU phyllochron interval, respectively).

There were three obvious exceptions across all cultivars to the narrow range of leaf appearance development rates discussed above. Two exceptions, characterized by low appearance rates, were associated with environmental stress. One was at GN in the summer of 2001, which included a period of severe drought, and the other was at OK in the summer of 2002, which included a period of very high water table. These two cases illustrated the sensitivity in leaf area development to environmental stress. Another exceptional case was at OK in the spring of 2001 in which the leaf development rates were recorded to be much higher than observed in other cases. We have no explanation for these high rates of leaf appearance.

There was only a 3% difference in the leaf appearance rate between the plant crop (0.0099 leaf TU^{-1}) and ratoon crop (0.0096 leaf TU^{-1}) although the difference was statistically significant ($P < 0.05$). The small difference between the plant and ratoon crop is consistent with the results observed by Robertson et al. (1998) in cv. Q117.

Leaf appearance rate of the early leaves (0.0101 leaf TU^{-1}) was greater than of the later leaves (0.0094 leaf TU^{-1}). While this 6% difference was significant ($P < 0.05$), this small difference is likely to be of little biological importance. Since the early leaves measured in the spring were typically leaves #1–12 and the later leaves were #15–25, previous studies with outdoor plants indicated that the differences would have been larger. The decrease in appearance rate of late leaves as compared to early leaves in previous studies was 14% (Robertson et al., 1998), 29–41% (Bonnett, 1998), and 55 and 69% (Inman-Bamber, 1994). On the other hand, the data of Campbell et al. (1998) with sugarcane grown in growth chambers did not indicate differences in appearance rate for leaves #10–28 for cultivars Q117 and Q138.

The explanation for the small difference in leaf appearance rate between early and late leaves in our study in contrast to some of the previous studies may reflect partially an artifact in previous field studies in regard to estimates of canopy temperature. Once crop leaf area has developed, evaporative cooling will cause the canopy to be 1–2 °C cooler than would be the case for a younger, more open canopy (Sinclair, 1971). Consequently, calculations of leaf appearance based on air temperature measured at a meteorological station will represent a relatively higher temperature for the mature leaf canopy than for the young, open leaf canopy. Therefore, the calculations of leaf appearance for the later leaves based on relative high temperatures could result in an estimated decrease in rate of leaf appearance expressed as a function of cumulative TU. While the temperature data in this study also relied on meteorological station data, the relatively open canopies and the very humid climate of Florida likely resulted in less of a relative temperature decrease than existed at locations in South Africa and Australia. Of course, the environmental controls of the chamber study of Campbell et al. (1998) would prevent any of the temperature deviations we hypothesize for field conditions and might explain the lack of change in leaf appearance in their study at later leaf stages. Detailed micrometeorological studies will be needed to fully resolve the temperature environment of the developing plant and differences under various climatic conditions and the possible influence on leaf appearance rate of early and late leaves.

There were differences among the four cultivars in their rate of leaf appearance (Table 1). Cultivar CP72-2086 had the slowest rate of leaf appearance among the tested cultivars. On the other hand, cultivar CP88-1762 had the greatest rate, although its rate of leaf appearance was only 3.9 and 6.6% greater than CP80-1743 and CP89-2143, respectively. These results did not, consequently, provide an explanation of the impression that CP80-1743 has the most rapid canopy closure.

The results reported by Bonnett (1998) for the Florida cultivar (CP51-21) could not be compared with the current results because previously the base temperature was assumed to be 8 °C. There was, however, considerable variability among cultivars in the study of Bonnett (1998) and CP51-21 was among the cultivars with the highest rate of leaf appearance.

Table 2
Shape factor to estimate area of individual leaves from measurement of leaf width and length

Cultivar	Shape factor	r^2
CP80-1743	0.711	0.95
CP88-1762	0.723	0.95
CP72-2086	0.705	0.96
CP89-2143	0.730	0.96

3.3. Leaf area development

The area of individual leaves was estimated by multiplying measurements of length × width. Since leaves are not rectangles, this calculation must be further multiplied by a 'shape' factor to account for differences in leaf shape. Robertson et al. (1998) reported a shape factor for cultivar Q117 of 0.62. The shape factors found in this study were greater than that reported by Robertson et al. (Table 2) and were consistent across cultivars. The average shape factor for all four cultivars was approximately 0.72 with a range from 0.70 for CP72-2086 to 0.73 for CP89-2143. In the calculation of leaf area for individual leaves, the shape factor appropriate for each cultivar was used.

Leaf area at each node increased in an approximately sigmoidal pattern as leaf number increased. There were differences among cultivars in the area per leaf with leaf number. As illustrated in Fig. 3, CP88-1762 had much greater leaf area than did CP72-2086 at the lower leaf numbers. Also, maximum area of individual leaves was reached at a much lower node in CP88-1762 than CP72-2086. CP88-1762 reached maximum area of individual leaves at approximately leaf #20 while CP72-2086 appeared not to reach maximum leaf area until about leaf #25.

Good fits ($r^2 \geq 0.88$) were achieved in regressions between individual leaf area and leaf number with the Gompertz equation used by Robertson et al. (1998) (Table 3). There were, however, differences among cultivars. As illustrated in Fig. 3, coefficient '*c*' in the equation was lowest for CP72-2086 among all cultivars at both locations, indicating the slowest increase in area as leaf number increased. Cultivar CP88-1762 had the highest increase in leaf area with leaf number at the OK site and equivalent to the other two cultivars at the EC site. The regression results indicated that

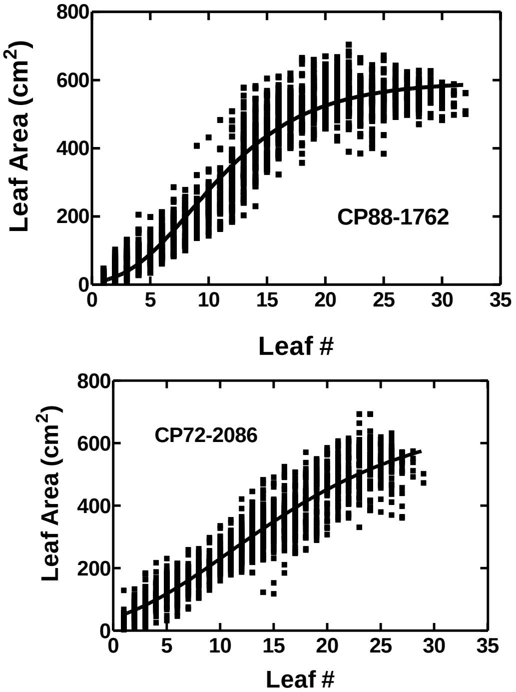

Fig. 3. Leaf area plotted against leaf number for all data collected from 60 plants each of cultivars CP72-2086 and CP88-1762 grown in 2001 at EC.

CP72-2086 might have the greatest maximum area per leaf, coefficient '*a*'. This may be an artifact of the analysis, however, since there was little data for this cultivar beyond leaf #25 and the value of '*a*' represents an extrapolation beyond the observed range of data. More extensive data for leaves #25–35 would help to resolve whether the slow increase in leaf area per node by CP72-2086 is truly compensated by larger leaves in the later leaves produced by the plant.

Table 3
Coefficients in model ($y = a\exp(-\exp(b - cx))$) to predict area (cm^2) of individual sugarcane leaves

Cultivar	a	b	c	r^2
EREC (2001)				
CP80-1743	547	1.66	0.188	0.87
CP88-1762	595	1.54	0.181	0.91
CP72-2086	690	1.04	0.095	0.88
CP89-2143	523	1.57	0.178	0.88
Okeelanta (2001)				
CP80-1743	527	1.6	0.172	0.88
CP88-1762	486	1.42	0.218	0.88
CP72-2086	665	1.14	0.105	0.84
CP89-2143	532	1.2	0.143	0.89

Leaf area production as a function of cumulative TU was calculated by combining the area of individual leaves (Table 3) and leaf appearance rate (Table 1). Due to uncertainty regarding the leaf appearance data for the spring at OK, the coefficients defining appearance rate that were obtained at this site in the summer were used. These calculations confirmed the differences among genotypes in leaf area production. Clearly, CP88-1762 produced a larger leaf area per stalk earlier in the development of the crop than the other cultivars tested. Assuming an equal number of stalks, the greater leaf area early in the season for CP88-1762 would be an advantage in the interception solar radiation and achievement of higher crop mass accumulation early in the season. These results may explain in part the increasing popularity of CP88-1762 in commercial plantings. On the other hand, CP72-2086 clearly had the lowest leaf area development and this result is consistent with purported slow development of a closed leaf canopy. CP80-1743 and CP89-2143 had similar patterns of leaf area production that were intermediate between the other two cultivars.

Overall, these results confirmed previous observations that the rate of leaf appearance is directly associated with air temperature. The leaf appearance results with the four cultivars developed in Florida had a base temperature and rate of leaf appearances that were not substantially different from the observations on sugarcane cultivars developed in Australia and South Africa. The critical observation highlighted in this study was the differences among cultivars in the area of individual leaves. In particular, there were marked differences in the area of individual leaves as the leaf number increased. Therefore, the main variant among the studied traits was the area of individual leaves produced during the early phases of the development cycle. The area of these early leaves could have a large influence on how rapidly the crop canopy developments and the amount of solar radiation that can be intercepted by the crop (Fig. 4). These results demonstrated a possible advantage for CP88-1762 in producing early leaves with larger leaf area. These results indicate that future breeding efforts might consider including selection of genotypes with leaves of large area early in the development cycle (leaves #5–15) as a trait contributing to high sugarcane yield.

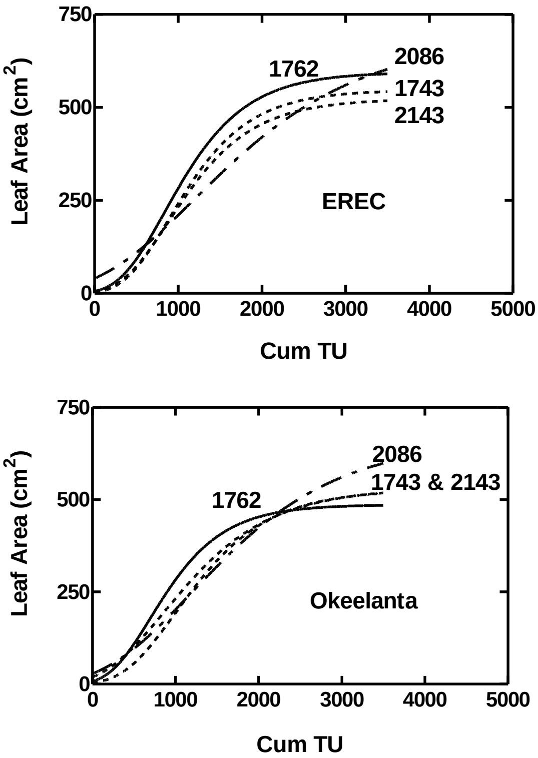

Fig. 4. Leaf area appearance plotted as a function of cumulative thermal units for each cultivar at EREC and Okeelanta.

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